HIGH RANKING FEMALES BIAS THEIR INVESTMENT IN FAVOUR OF MALE CALVES IN CAPTIVE AMMOTRAGUS LERVIA

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Short title: Biased maternal investment in Ammotragus

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SUMMARY

Calf suckling behaviour is a valid measure of maternal investment in the Saharan arrui, Ammotragus lervia sahariensis, since this variable is strongly correlated with the inter-birth interval. High ranking females allocate their resources preferably towards their sons, as the average suckling rate is significantly higher in male calves than in female calves during their first month of life, when maternal investment reaches the highest values of the whole lactation period. However, average suckling bout duration shows no sex differences. Some maternal behaviours, such as sniffing and licking, are strongly correlated with suckling events. Only during calves' first week does the mother assume the responsibility for maintaining proximity, but from the following week on the calves are the main responsible for maintaining it. In addition, when the calves are one month old, high ranking females tend to maintain a stronger link with their male calves. Female calves spend more time with their mothers than male calves during their first month of life, provided that the mother is holding a rank inferior to 60%; otherwise, the very opposite occurs, male calves being close to their mothers for longer, even from their first week of life. Finally, the higher the maternal rank the higher the proportion of male calves delivered.

Key words: Ammotragus, Ungulates, Parental Investment, Sex ratio

INTRODUCTION

According to Trivers and Willard's (1973) hypothesis on parental investment, in polygynous mammals those females in better physical conditions, i.e. with a greater ability to invest, should bias their investment towards male offspring, provided that son's reproductive success is mainly determined by maternal investment (Clutton-Brock and Albon 1982; Gomendio et al. 1990). There are two ways to accomplish this biased investment, either by allocating the resources preferably to one sex (Reiter et al. 1978), or by an adaptive adjustment of the sex ratio at birth (Trivers and Willard 1973); both strategies are not exclusive. Nevertheless, in those cases where maternal investment has a stronger effect on daughters' eventual reproductive success, natural selection will favour those mothers that invest more in their daughters, even when the variance in males' reproductive success is greater.

In social species, where hierarchical status plays a significant role, high ranking individuals benefit in many ways by having priority access to vital and reproductive resources (e.g. Clutton-Brock et al. 1984, 1986; Meikle et al. 1984; Bulger and Hamilton 1987; Wierenga 1990; Deutsch and Lee 1991; Johnson et al. 1991; Alados and Escós 1992); consequently, a relationship between social rank and reproductive success is expected.

Cassinello and Alados (1996) have recently pointed out that there is indeed a positive relationship between social rank and reproductive success in the Saharan arrui, Ammotragus lervia sahariensis, high ranking females giving birth to heavier sons than do low ranking ones (Cassinello 1994). In this paper I examine the secondary sex ratio and assess sex differences in relation to several maternal behaviours that reflect maternal care (see Clutton-Brock 1991), such as the proportion of time suckling, average suckling duration, sniffing and licking frequency, Hinde's proximity index (Hinde and Atkinson 1970) and proportion of time per sample that mother

and offspring spend together. My aim is to determine whether mothers holding high social ranks bias their care towards their sons, as could be expected on theoretical grounds.

METHODS

The Study Population

The population of Saharan arrui living in captivity in the Estación Experimental de Zonas Aridas, EEZA (Higher Council for Scientific Research, CSIC), Almería, Spain, comes from three founder individuals that were brought from western Sahara in 1975, two males and one female (Alados and Vericad 1993). Since then, and in spite of a high degree of inbreeding (Alados et al. 1988), the Saharan arrui has been breeding very successfully in Almería (see Cassinello 1994). At the present time there are five herds and 156 individuals. The study herd was made up by 17 males and 26 females at the beginning of the study, and 33 males and 43 females at the end of it. This herd has now become an all-males group, as the current EEZA management programme is primarily focused on preventing an excessive number of animals, inasmuch as re-introductions to the innative land are facing quite strong political difficulties. This subspecies used to be widespread over various localities in the North of Africa (see Gray 1985), but at present it is presumably extinct in the wild (Alados and Vericad 1993).

Sampling Method

Since the population of Saharan arrui was established in Almería, members of the staff of the EEZA are recording a series of data from every new-born: birth date, parturition type (single or twin), sex, body weight, identification of father and mother, and inbreeding coefficient (see Wright 1922; Ballou 1983). A number is also assigned to every animal using

plastic tags attached to their ears. During 1990, 1991 and 1992 I have been sampling behaviour in order to clarify the relationship between mother and offspring, according to the sex of the calf and the social rank of the mother. The social ranks of all the 16 lactating females of the study herd were calculated following the matrix method established by Scott (1980) and Lamprecht (1986) (Cassinello 1995).

During sampling I was able to monitor the whole herd from an elevation nearby, so the animals were not disturbed. I used a telescope to identify the individuals and a field computer Psion Organiser II to register a range of behaviours, which includes the ones mentioned below (see also Haas 1959; Habibi 1987).

Approaching and staring at refer to the same concept, i.e. an individual focusing his/her attention on other groupmate or a place; whereas departing implies leaving it. I have defined proximity as the approaching movement which leads to a distance between two arruis of one adult female body-length or less; whereas departure would occur when such movement leads to a distance of more than one body-length (Lickliter 1984; Ralls et al. 1987). Studying carefully every event I have defined as initiator of an action of proximity/departure the individual that, either by approaching/staring at or departing from another one, causes that both arruis end up at a distance of ≤ 1 or > 1 body-length, respectively. On the other hand, Hinde's proximity index (Hinde and Atkinson 1970) was used to assess who was mainly responsible for maintaining proximity, the mother or the calf. This index refers to the difference between the proportions of approaches and departures carried out by the calf, and it has been calculated for weeks and months, i.e. all the approaches and departures executed by mother and calf during calf's first week/month have been included in the calculation of a first value for the proximity index. This calculation was repeated for the second week/month and so on.

Grooming (licking and sniffing) and gnawing (a series of mild gnaws or chews usually carried out by the calves on their mothers or other calves, and which could be related to attachment) were other behaviours recorded to assess the relationship between mother and calf.

Samples were taken during the evening, when the animals were more active, notably adult females and calves (David Morgan pers. comm., pers. obs.). Focal sampling was used to record mother and calf behaviour (Altmann 1974; Martin and Bateson 1986), each sample being 20 minutes long. All the focals taken successively form a sampling period. Every female which gave birth during 1990, 1991 or 1992 was sampled four times a week during her calf's first two months of life; during the rest of the lactation period sampling was carried out 1.5 times per week. All mother-calf interactions and the ones between them and other groupmates were recorded during the focals. Also, during each sampling period, ad libitum sampling (Altmann 1974; Martin and Bateson 1986) was used to record all suckling and withdrawing events carried out by non-focal individuals, in order to assess more precisely both the maternal investment and hierarchical status, respectively. This sampling technique was possible due to the optimal conditions under which the animals were observed, which allowed me to monitor the whole herd without missing any conspicuous interaction, such as suckling and withdrawing. During focal sampling and every 5 minutes, the distance between the focal mother and her calf was registered, using a female adult body-length as unit (see above).

Suckling behaviour was assessed through two measures: suckling duration of each bout and proportion of time suckling per sampling period (the total suckling time divided by the total observation time), which is equivalent to Hass' (1990) average suckling rate, a term which is also used here. The other behaviours are represented by frequencies, i.e. the number of times an event occurred per minute, except the distance between mother

and calves, which is represented by the proportion of time spent at a particular distance (1, 2... body-lengths).

A total of 26 mother-calf pairs were sampled, of which 10 were twins (males:females = 4:6) and 16 single calves (9:7); but, due to stillbirths and early deaths, as well as a case of adoption (Cassinello, unpublished data), there were in practice 8 calves who shared their nursing with a sibling (4:4) and 18 single calves (9:9).

Analyses

Whenever possible parametric tests have been run, using in some instances transformations when the dependent variable was not normally distributed (Zar 1984). In order to use some continuous variables as factors in the analysis of variance, I had to form sub-groups or categories. This was the case of female social rank, which was divided in four ranking groups 0-29, 30-59, 60-89 and 90-100%. Starting from 16 females, the two highest ranking ones (ranks 90 to 100%) formed a group, based upon their distinctive behaviour (they were scarcely threatened by adult males; Cassinello, unpublished data); whereas the remaining females were distributed in equal size ranking groups: 0-29%, 30-59% and 60-89%, which included respectively five, four and five females. It is also noteworthy that the females from the lowest ranking group (0-29%) never gave birth to twins, and the ones from the 30-59% ranking group only gave birth to single calves or female twins (Cassinello, unpublished data). In some analyses, data of different calves from the same mother were considered as independent, because a previous analysis of the intra and inter-group variance showed for all the behavioural variables that the inter-group variance was not greater than the intra-group variance.

RESULTS

Parental Input vs Parental Investment

By definition, parental investment implies a reproductive cost for the parents (Trivers 1972). Therefore, whether the measure of parental input (sensu Evans 1990) implies an effect on fertility or not should be firstly determined. The relationship between the total lactation effort (the average suckling rate) and the interval of time to the next birth was analysed. Fig. 1 shows a strong and statistically significant relationship (the inter-birth interval was normally distributed): $N=8$, $R^2=0.91$, $p=0.0003$, the higher the average suckling rate, the longer the interval. Therefore, the suckling behaviour used should be considered as a reliable measure of maternal investment in the Saharan arrui.

Analysis of Suckling Behaviour

The analysis of suckling behaviour was assessed by means of both average suckling rate and suckling duration. To carry out parametric tests they were transformed into the logarithm and arcsine of the square root, respectively (Zar 1984). The changes of these variables over the total lactation period is shown in Fig. 2, from which the high values reached during the first month of a calf's life become evident (Student t test between months 0 and 1 for average suckling duration: $df=21$, $t=7.00$, $p<0.0001$; and proportion of time suckling: $df=21$, $t=8.80$, $p<0.0001$). This pattern shows that maternal investment was particularly important during a calf's first month, so that the following analyses were centred on this period.

The average suckling rate was significantly higher in one moth old males born to mothers holding social ranks ≥ 60% ($F(1,15)=7.55$, $p=0.01$); but when a mother held a rank lower than 60% there were no differences between male and female calves ($F(1,7)=0.07$, $p=0.80$) (see Fig. 3). Concerning average suckling duration, the analysis of variance did show no sex differences (maternal rank ≥ 60%: $F(1,14)=2.28$, $p=0.15$; maternal

rank < 60%: $F(1,7)=3.79$, $p=0.09$). From the calves' second month of life there were no sex differences either in maternal investment.

The grooming behaviour (sniffing and licking) performed by the mothers towards their calves was particularly frequent during the first days following the birth, decreasing thereafter (Spearman correlation: sniffing, $n=163$, $rho=-0.23$, $p=0.004$; licking, $n=163$, $rho=-0.49$, $p<0.0001$). This pattern was not followed by mother's gnawing behaviour ($N=163$, $rho=0.05$, $p=0.52$), which was markedly less frequent. Sniffing and licking were not related to maternal rank (sniffing: $F(1,24)=0.06$, $p=0.81$; licking: $F(1,24)=0.51$, $p=0.48$), nor to calf sex (sniffing: $F(1,24)=0.20$, $p=0.65$; licking: $F(1,24)=0.26$, $p=0.62$). The scarcity of data prevented testing these relationships for gnawing behaviour. By pooling the sniffing, licking and gnawing data I created a new variable which might be called "caressing", and which refers to the mother's care towards her calf. This variable was positively related to the average suckling rate ($N=26$, $R^2=0.24$, $p=0.01$).

Calves' gnawing behaviour addressed towards their mothers was relatively frequent during the sampling period, although a substantial decrease could be seen from the third month on ($N=172$, $U=2686$, $U'=3981$, $p=0.006$). During their first two months of life female calves born to low ranking (rank < 60%) mothers gnawed more frequently than male calves did, but the result was not statistically significant ($F(1,7)=0.87$, $p=0.38$); males and females born to high ranking mothers did not differ in their gnawing frequency ($F(1,15)=0.35$, $p=0.56$).

Study of Proximity and Spatio-Temporal Patterns

The study of proximity leads to two main questions: who is responsible for it and for how long is it mantained. To elucidate the first question I used Hinde's proximity index (Hinde and Atkinson 1970), which estimates the difference between the percentage of approaches and withdrawals carried

226 out by calves. It ranges from -1 to +1; the positive values denote a more
227 active role played by the calf, whereas the negative ones an active role
228 played by the mother. A value of 0 indicates that both, mother and calf, are
229 equally responsible for maintaining proximity. Concerning how long
230 mother and calf stay in proximity, I analysed the proportion of time that
231 they were at different distances (measured as adult female body-lengths).
232 The relationship between the weekly Hinde's proximity index and
233 calf's age is shown in Fig. 4. Only during calves' first week were mothers
234 responsible for maintaining proximity (analysis of variance for 0-7 weeks:
235 $F(7,83)=3.25$, $p=0.004$). During calves' first month of life a negative
236 relationship was found between Hinde's proximity index and maternal rank
237 for male ($N=11$, $R^2=0.40$, $p=0.04$), but not for female calves ($N=11$,
238 $R^2=0.002$, $p=0.91$) (see Fig. 5).
239 In order to determine the distances kept by mother and calf, an
240 analysis in which the proportion of time they were at different distances (0-
241 1, 2-3, 4-5, 6-10 and >10 body-lengths) was carried out. Throughout the
242 whole lactation period the proportion of time mother and calf were at a
243 distance of 0-1 body-lengths was not correlated with the average suckling
244 rate ($N=808$, $rho=0.05$, $p=0.18$); indeed, many suckling events took place
245 just after mother and calf had been several body-lengths away (pers. obs.).
246 On the contrary, being at a distance of more than 10 body-lengths
247 decreased the probabilities of a suckling event to take place ($N=808$, $rho=-$
248 0.07, $p=0.04$). On the other hand, when the calf was more than one body-
249 length away from its mother, grazing frequency increased ($N=814$, $rho=-$
250 0.23, $p<0.0001$). One week and one month old calves were found
251 predominantly at 0-1 body-lengths from their mother (Friedman's test for
252 first week: $df=4$, $\chi^2=21.47$, $p=0.0003$; first month: $df=4$, $\chi^2=66.63$,
253 $p<0.0001$). During calf's first month low ranking mothers (rank < 60%)
254 spent more time close to their calves than mothers of a higher status (see

Fig. 6; 0-1 body-lengths: $F(1,23)=8.60$, $p=0.007$; 2-10 body-lengths: $F(1,23)=4.45$, $p=0.046$; more than 10 body-lengths: $F(1,23)=1.61$, $p=0.22$). But after splitting the analysis by calf sex some differences were seen: male calves were found close to their mother more frequently than female calves provided that their mother's rank was ≥ 60% ($F(1,14)=5.16$, $p=0.04$). The opposite occurred when the rank was lower than 60%, i.e. female calves were found close to their mother for longer: $F(1,7)=6.44$, $p=0.04$) (see Fig. 7). Moreover, already one week old male calves born to high ranking females spent more time close to their mother than female calves ($F(1,15)=24.79$, $p=0.0002$).

Analysis of the Secondary Sex Ratio

The analysis of the secondary sex ratio (no. males/no. females, at birth) has an important drawback, as it does not include those mothers which have only delivered male calves. In order to prevent this, a first regression analysis was run to test whether the percentage of male infants depended on their mother's rank, whereas a second regression analysis tested the relationship between the absolute number of males and females delivered and their mother's rank. I considered individual females who contributed three or more offspring to the sample as well as the average ranks held by them (see Berman 1988), as rank may vary during the reproductive life (Cassinello 1995). The result of the analysis of the percentage of male calves was statistically significant ($N=10$, $R^2=0.42$, $p=0.04$), although the significance depended critically on just one data point (see Fig. 8). The absolute number of male calves was instead clearly related to maternal rank ($N=10$, $R^2=0.55$, $p=0.01$) (Fig. 9), but not the female calves ($N=10$, $R^2=0.005$, $p=0.85$) (Fig. 10).

The percentage of male infants was not related, on the other hand, to the mother's age ($N=10$, $R^2=0.12$, $p=0.33$), and did not differ significantly

between single and twin births (singles: 53% (N=164), twins: 45% (N=74); Mann-Whitney test: U=5555, p=0.30), so that we can assume that twinning has no effect on the sex ratio. Finally, calf sex was not related to the inter-birth interval either, as Student t test showed both for the sex of the previous birth (df=129, t=0.80, p=0.43) and the sex of the current birth (df=122, t=1.40, p=0.16).

In order to test the independence of the calf data, it was necessary to see whether calf sex depended on the sex of the previous calf. The term sex may refer to male or female in single births, and male/male, female/female or male/female in twin births, so calf sex and previous calf sex have five categories. The Kruskal-Wallis test was carried out. Calf sex was used as the grouping variable, whereas the number of births which follow the previous calf sex as the continuous variable. The null hypothesis establishes the same abundance of the five possible births, and the test was run five times, one for each of the categories of the previous calf sex. The hypothesis was not rejected, and the statistics corrected for ties were the same in the five occasions (Kruskal-Wallis test: df=4, H=4.0, p=0.41).

DISCUSSION

Introducing the Arguments

High social status facilitates priority of access to resources (mating, food), and diminishes risks by providing a more predictable social environment (Wilson 1975). As a direct consequence of this statement, high ranking individuals should be in better physical condition than low ranking ones (see, e.g., Iwamoto 1988; Soumah and Yokota 1991). In a previous study on the Saharan arrui, I pointed out the lack of a relationship between physical characteristics (body weight and length) and social rank in adult females (Cassinello 1995), an unexpected result, probably due to the

conditions of captivity, where food resources are constant. On the other hand, the phenotypic variables used might not be reliable enough to measure slight differences in the general welfare state of captive animals. Indeed, in this subspecies, high ranking females were primiparous earlier than low ranking ones (Cassinello 1994). This may well indicate a positive relationship between the nutritional state of an individual and the hierarchical position acquired, as nutritional state and age at first birth are usually negatively related (see Sadleir 1969; Bailey 1991). Moreover, behavioural evidence in the study population (stress, feeding preference, etc.; pers. obs.) and available empirical data in other ungulate species (Clutton-Brock et al. 1984; Lott and Galland 1987; Kojola 1989; Orgeur et al. 1990; Alados and Escós 1992) emphasize a positive relationship between social status and maternal investment. Thus, we could expect a differing maternal investment in female arruis of different social status, which may cause biased sex ratios at birth and a sex-biased investment (Trivers and Willard 1973; Clutton-Brock et al. 1981, 1984).

Mother's control of postnatal investment is high, for she nearly always determines average suckling duration (pers. obs.; see also Hogg et al. 1992). Only at a very early age, when calves are very weak and probably tire quickly, may they finish a suckling event spontaneously; although, under their mother's encouragement, they keep on suckling afterwards (pers. obs.; see however Birgersson and Ekvall 1994). It is also noticeable that the average suckling rate plays a predominant role in mother's control of the investment as compared with the suckling duration (see Hogg et al. 1992). The average suckling rate decreases with calf's age at a higher rate than average suckling duration, so that the former predominantly accounts for the decrease of maternal investment as in other mammals (White and Luick 1984; Gauthier and Barrette 1985; Robbins et

al. 1987; Stewart 1988; Becker and Ginsberg 1990; Birgersson and Ekvall 1994).

The average suckling rate is significantly higher during the first month of a calf's life than during the rest of the lactation period, decreasing uniformly from then on; but average suckling duration stops decreasing from the second month on (average=18 seconds). On the other hand, short-duration suckles are quite common during the first stage of lactation (pers. obs.), which may help to establish and maintain a close mother-calf bond by increasing olfactory, touching, visual and acoustic stimuli (Gubernick 1981; Prescott 1981).

Differing Behaviour of High Ranking Mothers towards Sons and Daughters

In this study high ranking mothers were shown to allocate more of their resources towards male calves, as the average suckling rate was significantly higher in sons than in daughters during their first month of life, when maternal investment reached the highest values of the whole lactation period. The maternal input measure (sensu Evans 1990) used, the average suckling rate, correlated with the inter-birth interval, so that it is a valid measure of maternal investment. This result supports other evidence of biased maternal investment found in the Saharan arrui, where high ranking females were shown to give birth to heavier males than low ranking ones (Cassinello 1994).

In relation to the sniffing behaviour, Horejsi (1976, in Hass 1990) suggests that those mothers which frequently sniff their calves are better mothers, confering a higher survival rate on them. Hass (1990), however, states that this sort of behaviour may indicate, at most, a degree of maternal "attentiveness" towards her calves, without necessary indicating the quality of maternal care. A clear distinction between terms like "care" and

"attention", and "maternal investment" must be taken into account, in order to prevent confusing simple maternal caring behaviours, which do not imply reproductive costs, with actual investment. In the Saharan arrui, grooming behaviours are correlated with the average suckling rate, which may imply some relationship between these events and the degree of investment given to the calves.

It has also been found that high ranking females spend more time with their sons than with their daughters and are more willing to maintain proximity to them; but it is premature to assume that these behaviours also reflect maternal investment, as there is no evidence about their reproductive costs. The significant bias in favour of sons in high ranking mothers reflects preferential investment, and therefore also indicates the tendency, confirmed above, towards higher investment in male calves.

High and Low Ranking Mothers Differing as a Group

The second issue to be considered here is that high ranking females deliver a greater proportion of male calves than low ranking ones, so that Trivers & Willard's (1973) postulate on polygynous mammals is fulfilled, i.e. the adaptive adjustment of the sex ratio at birth. This has already been shown in other species (e.g. Clutton-Brock et al. 1984; Meikle et al. 1984). On the other hand, the lack of any relationship between calf sex and the following inter-birth interval means that the cost of raising either sexes does not vary significantly under captive conditions (cf. e.g. Gomendio 1990).

The results obtained also show a clear distinction between high and low ranking mothers when allocating the resources to their calves. While high ranking mothers are more discriminating as a function of calf sex (see above), low ranking ones are not, as they equally invest in sons and daughters. Interestingly, no particularly high aggression level on low ranking mothers has been seen in the study population (Cassinello 1994),

even when splitting the analysis by calf sex (Cassinello, unpublished data), so that Gomendio's (1990) arguments on rhesus macaques cannot be applied here, as the differences on the level of maternal investment in mothers of differing social status in the Saharan arrui depend on the energetic demands of rapidly growing sons, and not on the level of aggression suffered by the mothers (see Clutton-Brock et al. 1984; Gomendio 1990).

Conclusion

Following Byers and Moodie (1990), the degree of sexual dimorphism (1.96) and mother-calf average body weight ratio (0.160) of the Saharan arrui would include this subspecies in the group of polygynous ungulates which show biased maternal investment according to Trivers and Willard's (1973) hypothesis. Indeed, the statiscally significant difference between the two groups differentiated by Byers and Moodie (1990) is retained after adding the arrui data (Mann-Whitney test: N=12, U=4, U'=32, p=0.02).

Finally, the investment allocated to sons of high ranking mothers is not particularly greater than that of low ranking ones (see Fig. 3). This raises the question of a hypothetical difference in the "quality" of investment by high and low ranking females. I have no data either to refute or confirm this possibility, so that the question remains open; but, whatever the answer may be, my statement of sex-biased investment in high ranking females would still be valid.

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FIGURE LEGENDS

Fig. 1. Relationship between the average suckling rate during the whole lactation period and the interval of time to the next birth.

Fig. 2. Monthly suckling behaviour: duration (a) and suckling rate (b).

Fig. 3. Suckling rate (mean + SE) of one month-old calves, for two maternal rank groups and according to calf sex.

Fig. 4. Weekly values of Hinde's proximity index (mean + SE).

Fig. 5. Relationship between monthly Hinde's proximity index during calves' first month, and maternal rank. The continuous regression line corresponds to male calves and the discontinuous one to female calves.

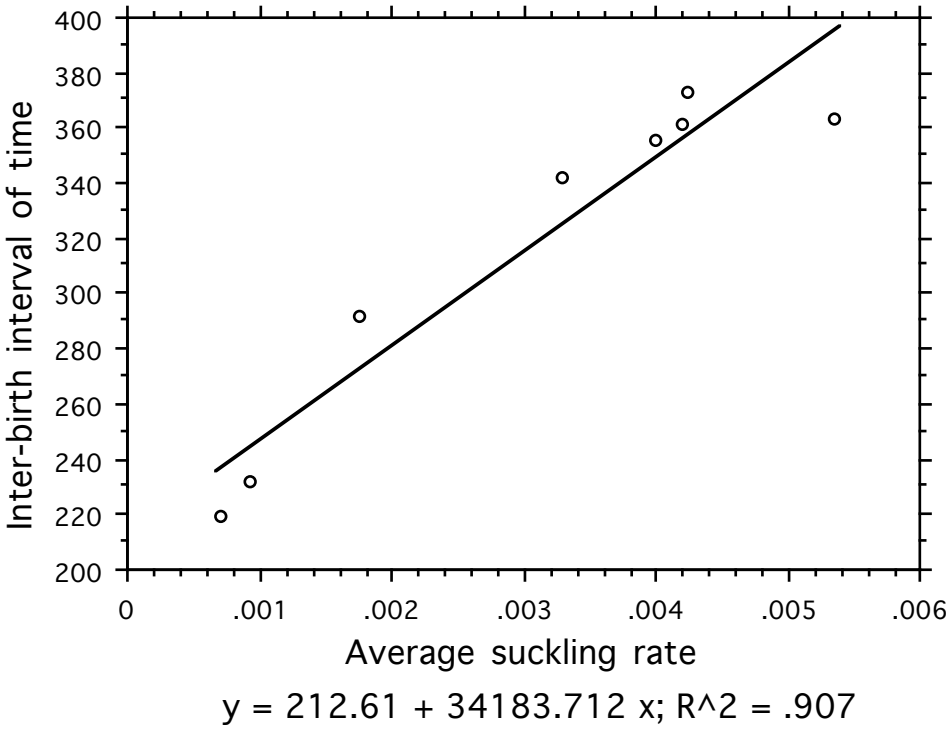
Fig. 6. Proportion of time (mean + SE) per sample spent by mothers and calves at different distances (in body-lengths) during calves' first month of life, and for two maternal rank groups.

Fig. 7. Proportion of time (mean + SE) per sample spent by mothers and calves at 0-1 body-lengths during calves' first month, according to calf sex and for two maternal rank groups.

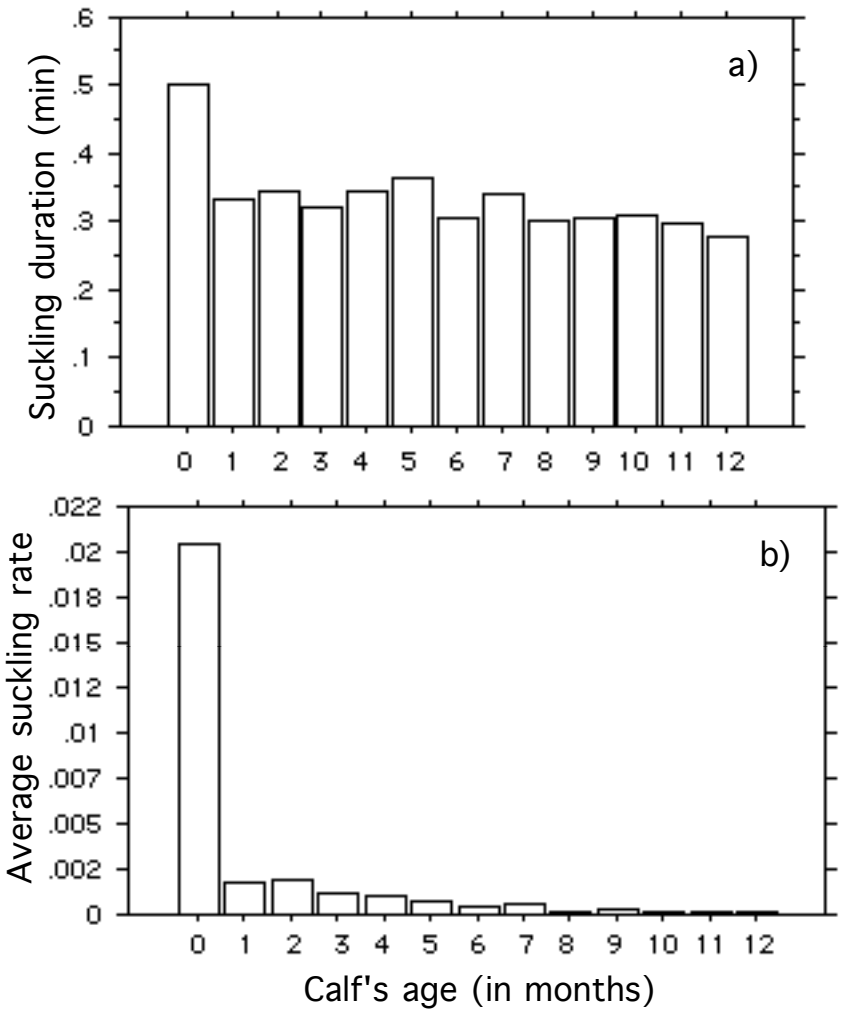
Fig. 8. The percentage of male calves produced by individual females as a function of the average maternal rank.

Fig. 9. The number of male calves produced by individual females as a function of the average maternal rank.

Fig. 10. The number of female calves produced by individual females as a function of the average maternal rank.



J CASSINELLO - FIGURE 1



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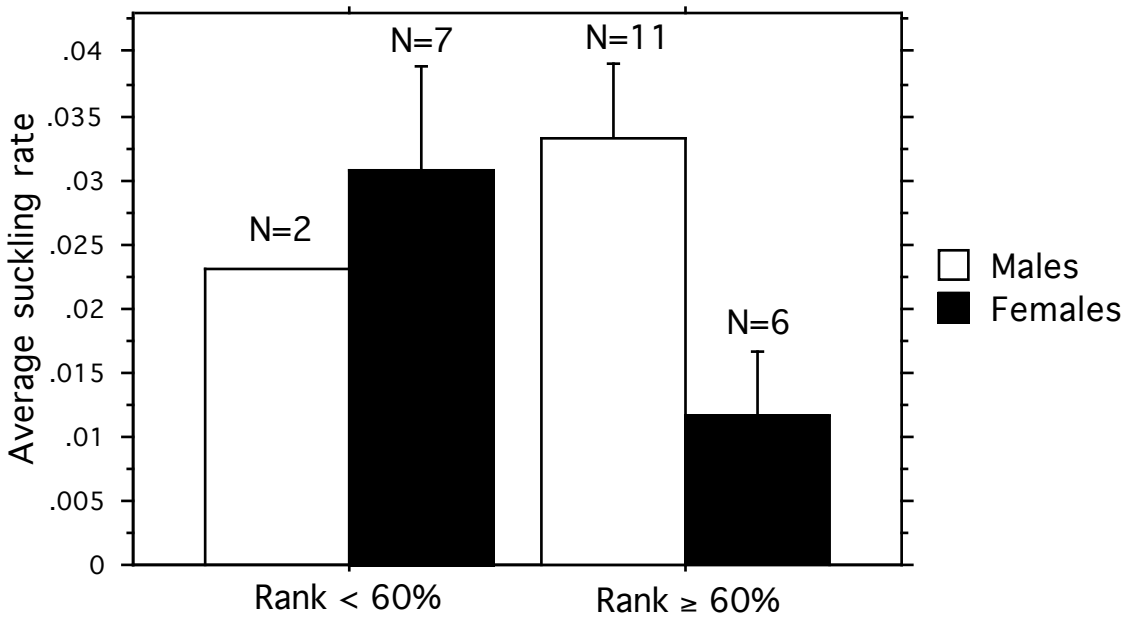

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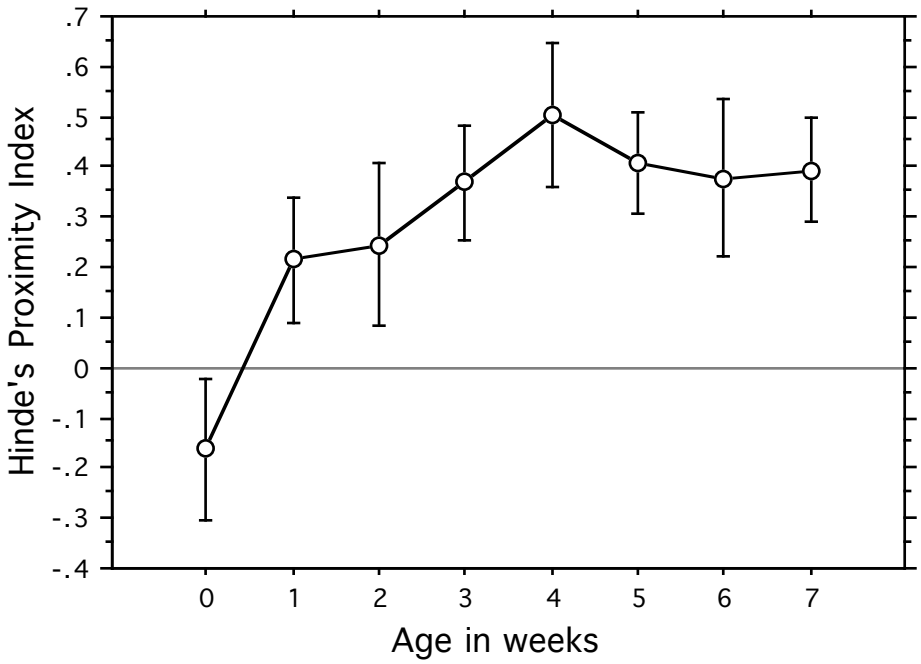

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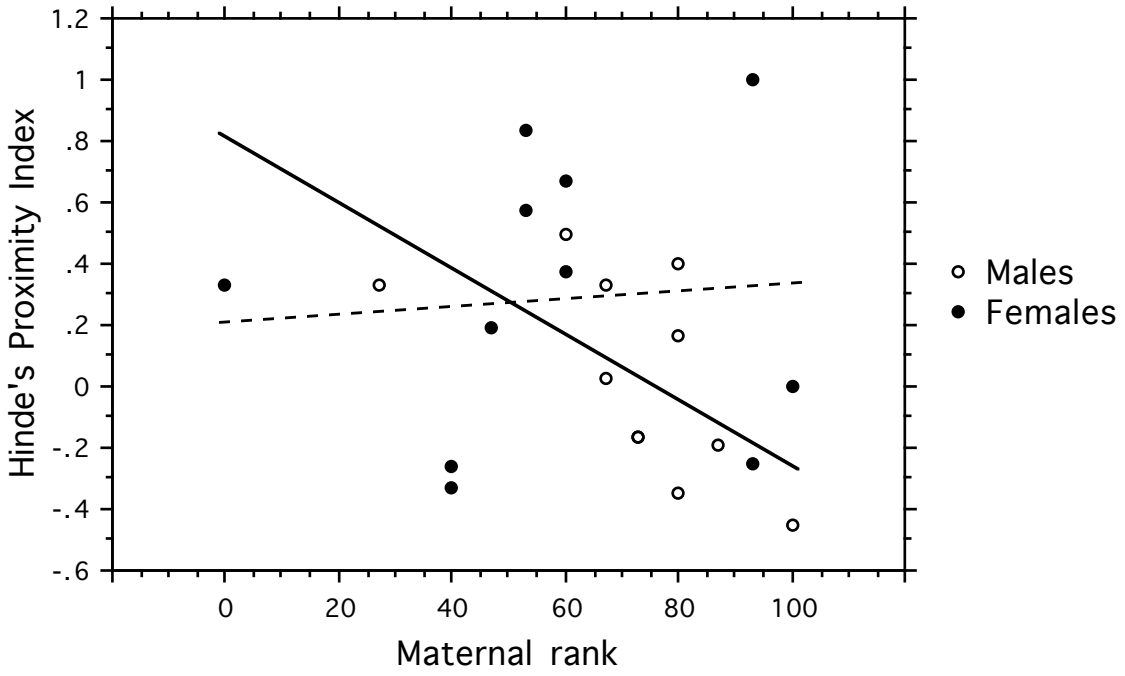

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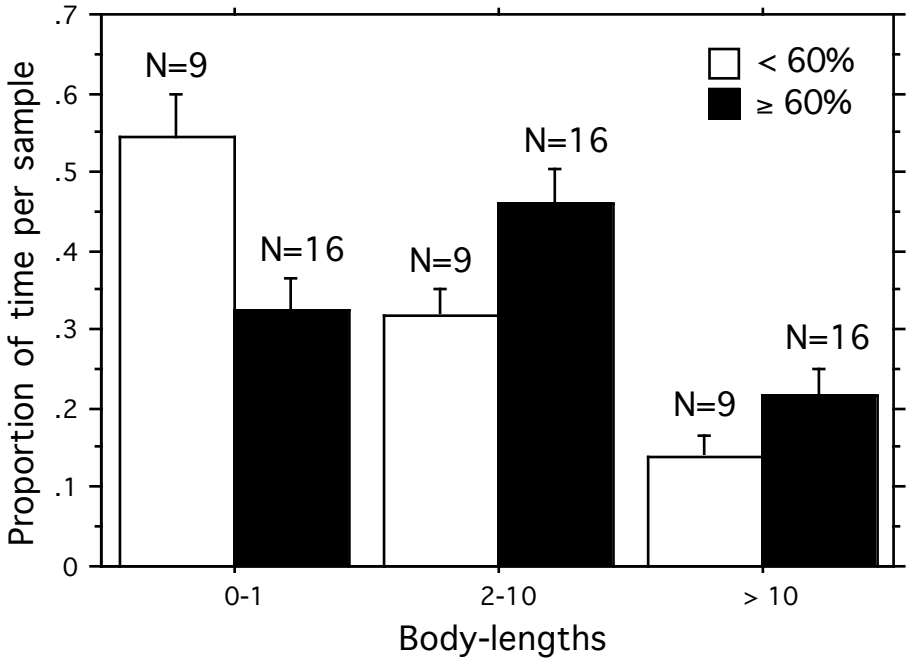

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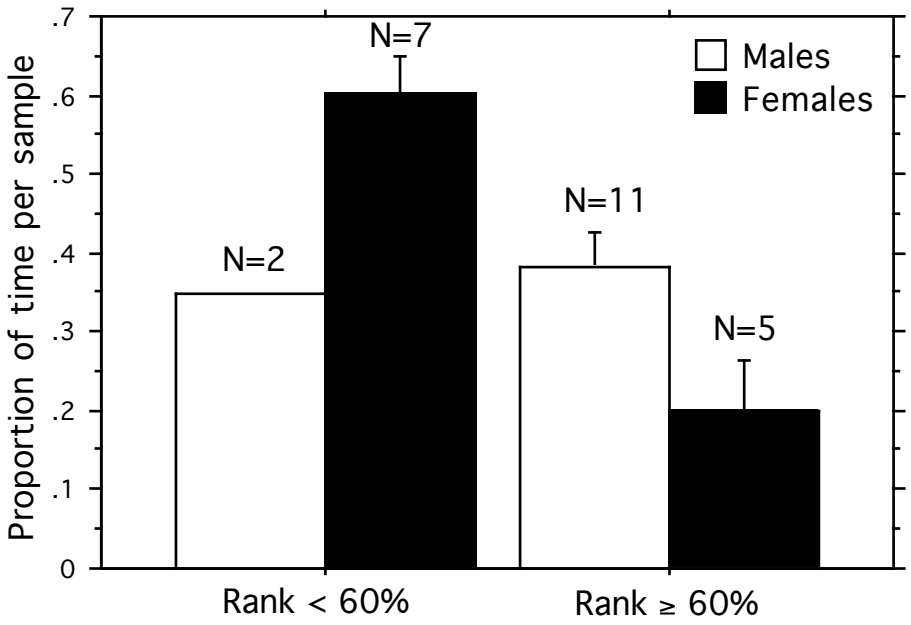

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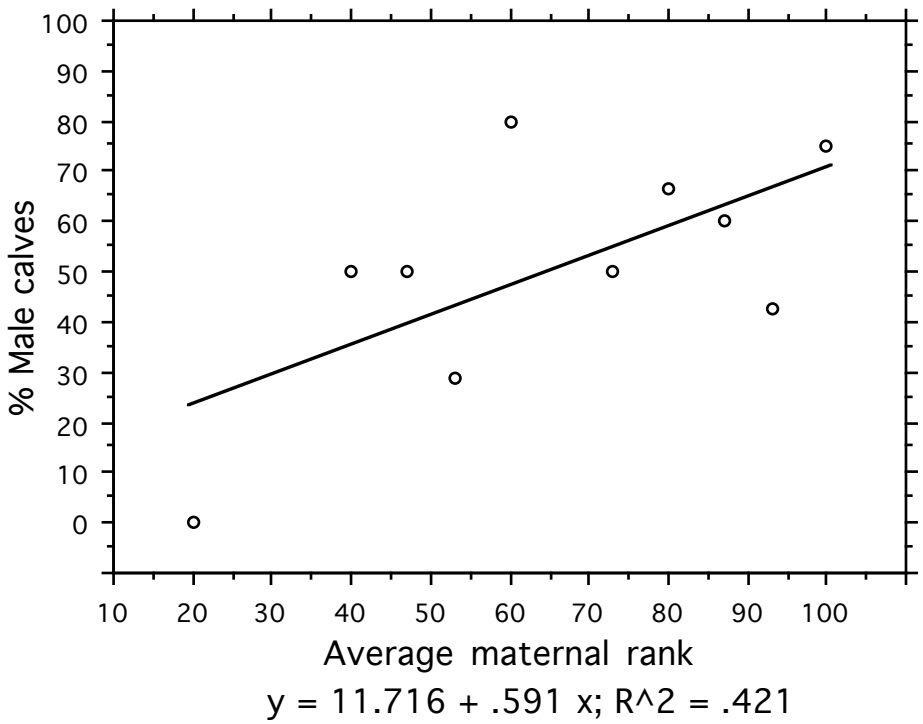

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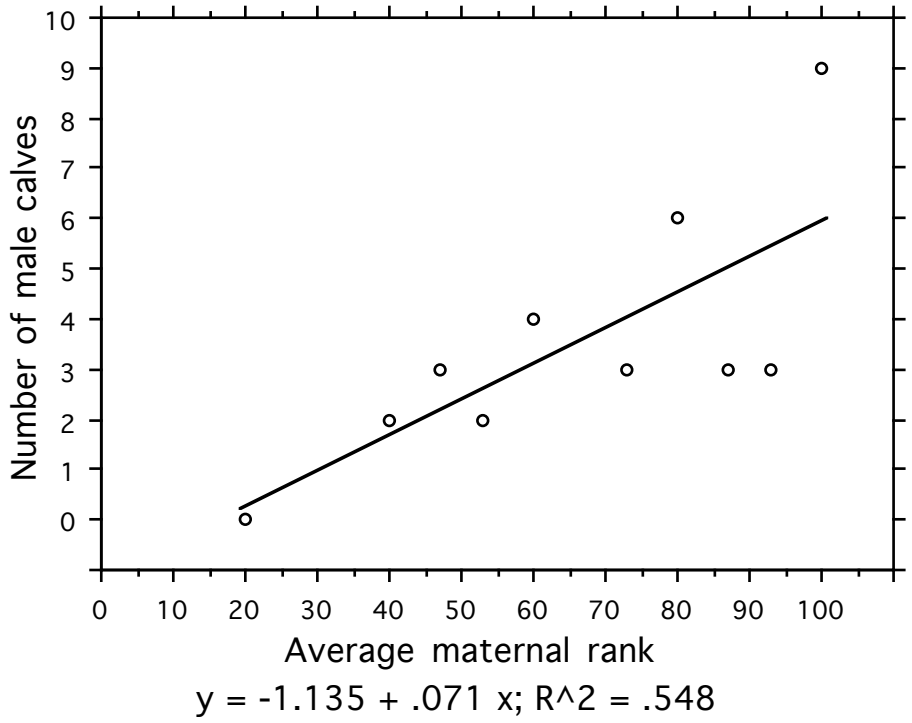

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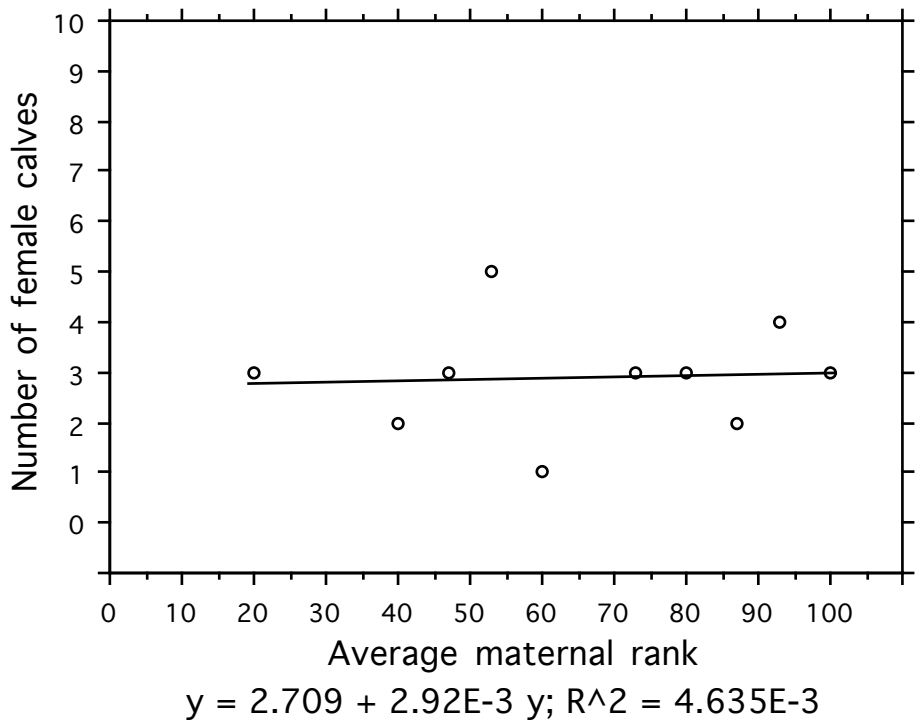

J CASSINELLO - FIGURE 10